VESTIBULAR REACTIONS IN CAT AND MAN DURING AND AFTER ANGULAR ACCELERATION. I. RESPONSES FROM THE LATERAL AND THE VERTICAL CANALS TO TWO STIMULUS DURATIONS

William E. Collins and Fred E. Guedry, Jr.



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NAVAL AEROSPACE MEDICAL INSTITUTE

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### VESTIBULAR REACTIONS IN CAT AND MAN DURING AND AFTER ANGULAR ACCELERATION. I. RESPONSES FROM THE LATERAL AND THE VERTICAL CANALS TO TWO STIMULUS DURATIONS\*

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### SUMMARY PAGE

### THE PROBLEM

Neurophysiological responses of cats are frequently studied in an attempt to understand perceptual and physiological responses of men. The purpose of the present experiments is to compare nystagmus responses of man and cat to equivalent vestibular stimuli to provide a basis for comparative interpretation of data.

### **FINDINGS**

Recordings of ocular nystagmus were obtained in darkness from cats and human subjects to 4-deg/sec<sup>2</sup> angular accelerations about an Earth-vertical axis. Results showed greater primary and secondary nystagmus for stimulation of lateral canals than for stimulation of the vertical canals. In cats, both lateral- and vertical-canal responses to a 36-second stimuli peaked after 15-21 seconds of angular acceleration, and this was followed by a steady decline. Declines during acceleration were not apparent in nystagmus of human subjects. Cats consistently demonstrated secondary nystagmus whereas humans did not. After termination of acceleration, primary nystagmus from cats lasted longer and exhibited a greater number of eye movements following an 8.4-second stimulus than following a 36-second stimulus. In humans, a like difference occurred in the sensation but was not present in nystagmus. In this regard, nystagmus from cats resembled the subjective reactions of man more than they did the nystagmus of man.

### **ACKNOWLEDGMENTS**

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### INTRODUCTION

During prolonged angular acceleration inertial torque deflects the cupula, but the deflection is eventually balanced, primarily by the cupula's elastic restorative force. If cupula displacement from its position of static equilibrium controls the magnitude of vestibular reactions, a prolonged angular acceleration should, according to the "torsion pendulum theory" (11,21), yield an increasing response for about 20-30 seconds; this response level should be maintained without decline as long as the angular acceleration continues. Several authors (9, 10, 13, 18, 19) have reported that the subjective velocity rises and declines during prolonged angular acceleration, contrary to theoretical expectations. Guedry and Ceran (13) showed that the temporal period required for the subjective reaction to peak (and then decline) was about constant (27 seconds) for angular accelerations ranging in magnitude from 0.5 to 2 deg/sec<sup>2</sup>. Subsequent experiments (Guedry and Cunat, unpublished) showed this to be true for stimuli up to 4 deg/sec<sup>2</sup>.

The present experiments seek to compare cat and man in regard to several characteristics of the nystagmus response elicited by two durations of a 4-deg/sec<sup>2</sup> angular acceleration.

### **PROCEDURE**

**CATS** 

### **Apparatus**

The Huffman Rotation Device (6), located in a lightproof room, was used to produce acceleration programs. Animals were tested on the rotator in pairs with their heads at the center of rotation. One cat box was secured to runners on the turntable and the second box was secured to a framed tier arrangement above the first box (7).

### Restraint

Cats were restrained by the method of Henriksson, Fernández, and Kohut (16). Three or more days prior to testing, the animals were anesthetized and holes were drilled transversely through their canine teeth. At the same time, fur around the ocular orbits was shaved off and a guideline for positioning the head was drawn with washable ink from the canthus to the tragus on each side. For testing, each animal was wrapped in a towel and placed in a cat box. A strand of piano wire was inserted through the holes in the canine teeth. The wire was fastened securely and the head of the animal was positioned by means of an adjustable device on the front of the box.

### Recording

For recording horizontal components of eye movements, needle electrodes were inserted by the outer canthi. Vertical components were obtained by means of surface electrodes taped above and below the left eye. The recorder was an Offner Type R

dynograph with three-second time constants used in amplification. Prior to testing, animals were placed in an optokinetic stimulator; a drum speed of 24 deg/sec was used to obtain data for calibration purposes.

### **HUMAN SUBJECTS**

### **Apparatus**

A Stille-Werner RS-3 rotating chair, situated in a lightproof room, provided the acceleratory stimuli for the human subjects.

### Recording

A pair of surface electrodes, taped by the outer canthi of the eyes, detected horizontal eye movements, while a second pair was positioned above and below the left eye for the recording of vertical eye movements. An Offner Type T polygraph with a three-second time constant was used in amplifying and recording the eye movement signals. Eye calibrations were obtained prior to each test by means of a calibration chart located on one wall of the rotation room.

### **METHOD**

Each of eight cats and eight human subjects received two angular accelerations (for 8.4 and 36 seconds) stimulating the lateral semicircular canals. The same durations were used for the vertical canals. Stimuli were 4-deg/sec<sup>2</sup> accelerations and decelerations separated by 54 seconds of constant velocity for cats and by 120 seconds of constant velocity for humans. In cats, vertical canal stimulation was accomplished by placing each animal on its right side to locate its sagittal plane at the center and in the plane of rotation; human subjects leaned forward with the head turned to place the sagittal plane of the skull in the plane (and at the center) of rotation. A biteboard and headrest assisted in this positioning. Stimuli were presented in a counterbalanced order as indicated in Table 1.

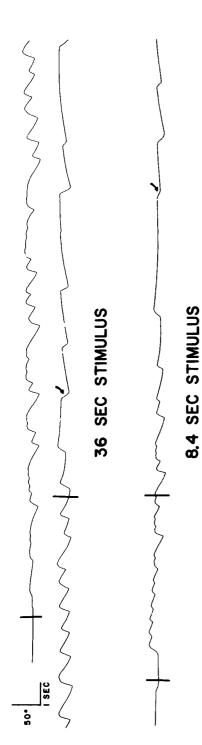
Neither the cats nor the human subjects had been used in previous vestibular experiments. For the humans this necessitated instruction regarding the signaling of subjective events without actual practice in making such judgments; they reported onset and cessation of apparent rotation by means of a signal key.

### RESULTS AND DISCUSSION

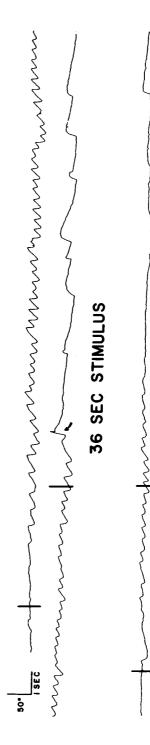
### **CATS**

The eight animals received only four trials (two lateral and two vertical canal stimulations) on the first day. Some examples of recorded nystagmus appear in Figure 1. The critical portion of the response for several purposes of this study began at the end of each stimulus. Thus, time measurements were made from the end of each stimulus

# CAT NO. 100 (HORIZONTAL NYSTAGMUS)



## CAT NO. 105 (VERTICAL NYSTAGMUS)



### 8.4 SEC STIMULUS

Figure 1

Nystagmus Recorded from Two Cats for Two Durations of 4-deg/sec<sup>2</sup> Angular Acceleration

to a) the end of the primary response and b) the start of the secondary nystagmus. The number of beats of primary nystagmus which followed stimulus termination was also tabulated. These data appear in Table II. In 47 of the 48 comparisons the primary poststimulus response to the 8.4-second stimulus exceeded that of the 36-second stimulus.

Table I

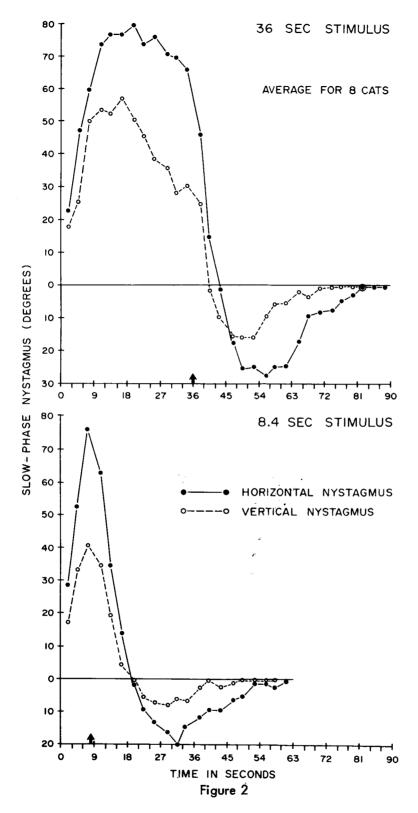
Order of Stimulus Presentation\*

Human		Rotation		Trial	s	
Subjects	Cats	Direction	1	2	3	4
Or, Wa	100, 101	CW	8.4 L	36.0 L	8.4 V	36.0 V
Nu, Jo	102, 103	ccw	36.0 L	8.4 L	36.0 V	8.4 V
Pe, Me	104, 105	CW	8.4 V	36.0 V	8.4 L	36.0 L
Fr, Ma	106, 107	ccw	36.0 V	8.4 V	36.0 L	8.4 L

<sup>\*</sup>All trials comprised stimuli of 4 deg/sec<sup>2</sup>. Duration of the stimulus was either 8.4 or 36 seconds. L and V refer, respectively, to lateral and vertical canal stimulation.

Plots of the complete nystagmic responses to the 8.4- and the 36-second stimuli appear in Figure 2. Slow-phase output was scored by summing the vertical displacements of beats from peak to baseline for successive three-second intervals. Greater output of primary nystagmus is evident for the lateral canals, as compared with the vertical canals, for both stimulus durations. For the 8.4-second stimulus, primary nystagmus increased throughout the stimulus period for both the "horizontal" and "vertical" curves. For the 36-second stimulus, there was a marked peaking in the response to stimulation of the vertical canals during the 15-18-second interval and a steady decline of that response throughout the remainder of the stimulus. For stimulation of the lateral canals during the 36-second stimulus, peaking occurred in the 18-21-second interval and was followed by a lesser decline than that noted for the vertical canals.

Secondary nystagmus is also plotted in Figure 2. Secondary nystagmus was obtained from each cat for each stimulus condition with one possible exception (the secondary response to vertical canal stimulation was weak and unscorable in cat No. 100). For both vertical and lateral canal responses the 36-second stimuli produced greater secondary responses than did the 8.4-second stimuli. In addition, horizontal secondary nystagmus showed greater output than vertical secondary nystagmus by



Time-Course Plots of Slow-Phase Eye Displacement in 3-sec Intervals for 8 Cats

Arrows indicate termination of acceleration. Points above the zero line represent primary nystagmus; points below the zero line represent secondary nystagmus.

Table II

Measures of Primary Nystagmus Following the Termination of Each Rotatory Stimulus for Cats\*

	Time from End of Stimulus to	m End o	f Stimul	us to End	Time from	End of S	Time from End of Stimulus to Start of Secondary Nystaamiis (seconds)	Start	Beats o	Beats of Primary Nystagmus offer End of Stimulus	/ Nystag mulus	mus
Cat	or rrimary Lateral	ary rys eral 36	or rrimary lystagmus (secon Lateral Vertical 8.4 36 8.4 36	vs (seconds) Vertical .4 36	Lateral 8.4	ary 1473 36	8.4	Vertical	Lateral 8.4 3	əral 36	8.4	Vertical
001	9.2	2.5	6.5	0.5	12.9	5.7	1.1	3.4	<b>ω</b>	2.8	9.0	1.0
101	11.4	7.0	7.9	7.0	14.4	8.7	9.1	4.6	14.8	10.0	11.5	7.8
102	3.2	0.5	25.7	5.7	6.0	0.9	28.3	9.0	3.3	0.5	18.5	4.0
103	4.9	4.4	8.8	4.2	8.	6.3	18.1	6.2	3.5	1.5	7.5	3.5
104	10.7	5.4	8.2	3.1	12.0	9.9	10.9	3.9	& &	2.0	7.0	2.5
105	13.8	6.9	13.6	3.0	15.8	10.4	14.6	4.3	14.5	8.0	10.0	2.8
8	11.5	5.7	6.0	8.4	14.7	7.0	7.7	7.2	10.0	4.5	5.5	4.5
107	10.9	8.2	6.0	-1.5#	14.6	11.0	17.5	3.7	7.5	6.0	6.5	-
 <b>∑</b>	9.5	5.1	10.3	3.4	12.3	7.1	14.7	5.9	8.9	4.4	9.4	3.4

<sup>\*</sup>Each response value is a mean of responses to an acceleration and a deceleration stimulus. Stimuli were 4 deg/sec<sup>2</sup> for either 8.4 or 36 seconds.

#Nystagmus ended during stimulus.

amounts proportional to differences in their respective primary reactions. Further, the mean peak of the secondary response occurred 21 to 24 seconds after the end of the 8.4- and 36-second stimuli for horizontal nystagmus, and 15 to 21 seconds after the 8.4- and 36-second stimuli for vertical nystagmus.

To pursue further the relationship of secondary to primary nystagmus and the effects of prolonged stimuli on those responses, six of the animals were given, one day later, a series of fifteen trials stimulating the lateral canals with the 4-deg/sec<sup>2</sup> stimulus for a 36-second duration. Tracings for trials 1, 5, 10, and 15 were scored and the data plotted in Figure 3. With repeated stimulation a marked depression of both the primary and secondary response curves occurred, peaking of the response was followed by a decline in nystagmic output during the remainder of the stimulus, and the peaks of both primary and secondary nystagmus shifted toward earlier occurrences (4).

### **HUMAN SUBJECTS**

d j

Eight human subjects (four males and four females) were given stimulations identical to those administered to the cats. Nystagmus data were also scored similarly and appear in Table III. Some examples of nystagmus tracings are presented in Figure 4. In addition, duration of the sensation of turning was calculated from the end of each stimulus to the end point of the sensation (Table IV).

In twenty of the forty-eight comparisons (Table III) human responses to the 36-second stimulus exceeded responses to the 8.4-second stimulus (nine of these cases were for the "number of beats" measure), and although the mean group data for "duration of primary nystagmus" were longer for the 8.4-second stimulus, the differences were slight. Mean number of beats of primary nystagmus following stimulus termination actually favored the 36-second over the 8.4-second stimulus, but the differences were not significant. Thus, results obtained from the cats, in which the poststimulus nystagmic responses to the 8.4-second stimulus consistently exceeded those of the 36-second stimulus, were not borne out in the data from human subjects.

Human subjective data (Table IV) in eleven of thirteen comparisons (three comparisons were not obtained) showed that the 8.4-second stimulus resulted in sensations of longer duration after termination of angular acceleration than did the 36-second stimulus. For two subjects the sensation to vertical canal stimulation ended during the 36-second stimulus.

Time plots of the nystagmus recorded during the two stimulus conditions appear in Figure 5. Responses from the lateral canals were of greater magnitude than those from the vertical canals. No clear peaking or decline in output during the stimulus appeared for either set of canals. Secondary nystagmus is plotted in the same figure. However, secondary responses were questionable and unscorable in six men to the 8.4-second lateral canal stimulus, in five men to the 8.4-second stimulus to the vertical canals, in three men to the 36-second vertical canal stimulus, and in one man to the 36-second lateral canal stimulus. Thus, in two general respects, human data

Table III

Measures of Primary Nystagmus Following the Termination of Each Rotatory Stimulus for Human Subjects\*

	i	To Landing to End	Cotton	to Fnd	Time fr	Time from End of Stimulus to Start	Stimulus to	o Start	Beats o	Beats of Primary Nystagmus	Nystagn	กบร
	ime t		בטוטשווכ ד	10 Ella	Jes Jo	of Secondary Nystaamus (seconds)	staamus (se	conds)	affe	after End of Stimulus	itimulus	
	ot Prin	of Primary Nystagmus (seconds)	ses) snubc	(spilds)	-	l ateral	Vertical	cal	Lateral	힏	Vertical	ical
	, La	Lateral 34	Vertical	.cal	8.4	8	8.4	3%	8.4	8	8.4	8
Subject	10 6	-	2   2	7 7	32.9	26.5	55.2	13.4	18.5	14.5	15.0	9.0
Ž	/- 47	. 0		) i		7 76	0	0	92.0	61.5	25.5	23.0
ŏ	29.8	34.7	- 9	c. 97	97.0	0.00	?	2			•	C
Me	32.0	25.4	16.0	14.6	38.6	32.1	24.2	16.5	25.0	24.5	13.0	y.5
۸a	42.4	33.0	8.5	10.5	48.1	38.6	13.6	14.9	23.0	32.5	5.0	10.5
e e	18.2	23.2	6.2	11.2	21.6	24.5	8.6	19.2	9.5	21.0	2.5	9.5
<u>.</u>	36.2	30.4	22.4	9.0	39.8	30.1	15.8	14.5	38.5	45.5	16.0	13.0
<u>.</u> 9	37.1	36.1	15.8	4.9	36.6	32.6	1	8.0	36.0	47.5	6.5	7.0
Σ	41.0	38.8	4.6	13.7	41.4	43.0	20.2	17.1	54.5	77.5	7.5	10.5
<b>"</b> <b>≥</b>	32.7	30.1	14.4	12.3	36.4	33.0	21.2	14.1	37.1	40.6	11.4	11.5

\*Each response value is a mean of responses to an acceleration and a deceleration stimulus. Stimuli were 4 deg/sec<sup>2</sup> for either 8.4 or 36 seconds.

Table IV

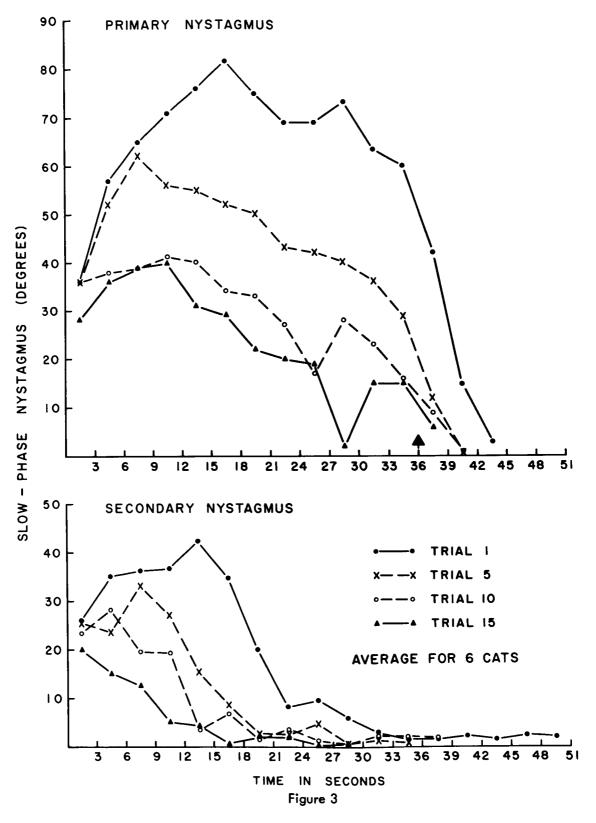
Time in Seconds from End of Each Rotatory Stimulus to End of Subjective Turning

Experience for Human Subjects\*

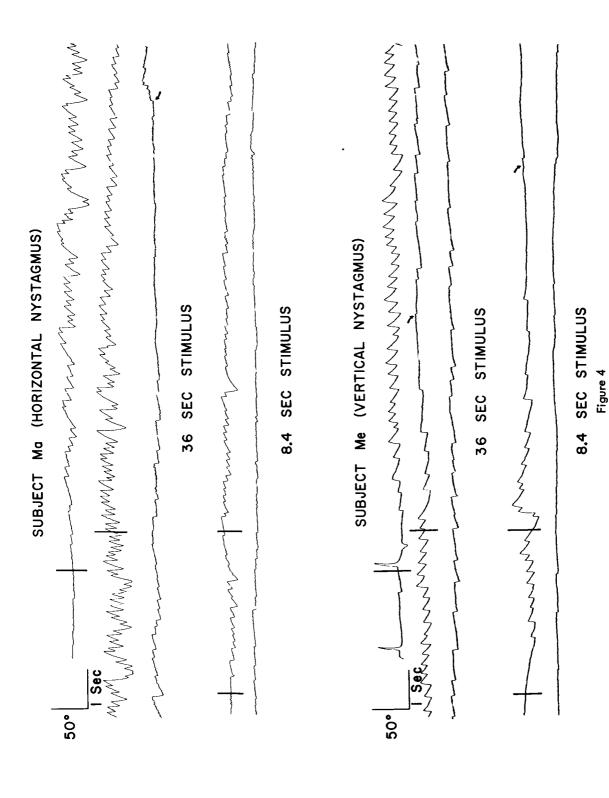
		Vertical	Canals
8.4	36	8.4	36
-	-	-	-
-	29.5	12.5	9.3
34.5	12.4	44.0	9.2
27.8	14.9	10.4	23.7
11.0	7.7	7.7	2.0
23.1	14.3	11.5	28.6
20.4	12.4	19.9	-1.3#
7.7	3.1	7.4	-15.1#
20.8	13.3	16.2	8.1
	8.4 - 34.5 27.8 11.0 23.1 20.4 7.7	29.5 34.5 12.4 27.8 14.9 11.0 7.7 23.1 14.3 20.4 12.4 7.7 3.1	8.4       36       8.4         -       -       -         34.5       12.4       44.0         27.8       14.9       10.4         11.0       7.7       7.7         23.1       14.3       11.5         20.4       12.4       19.9         7.7       3.1       7.4

<sup>\*</sup>Each value is a mean for an acceleration and a deceleration stimulus. Stimuli were  $\frac{4}{2} \frac{1}{2} \cdot \frac{$ 

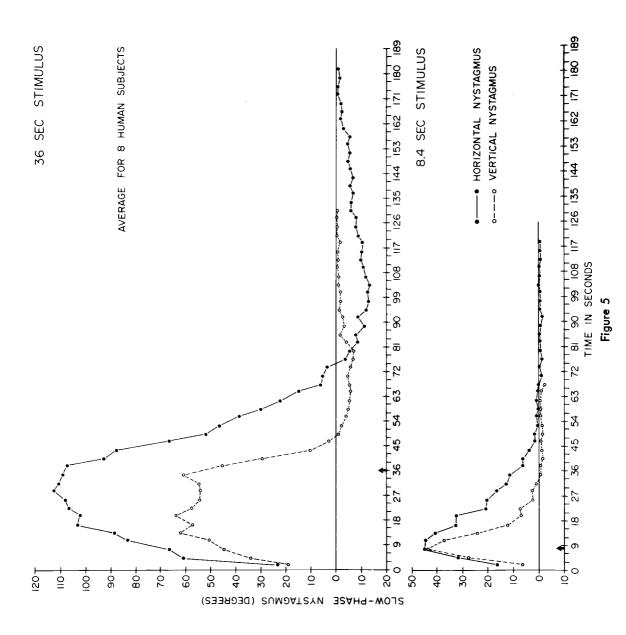
<sup>#</sup>Subjective turning experience ended during stimulus.



Time-Course Plots of Slow-Phase Eye Displacement for Trials 1, 5, 10, and 15 of the Habituation Series



Nystagmus Recorded from Two Human Subjects for Two Durations of 4-deg/sec<sup>2</sup> Angular Acceleration



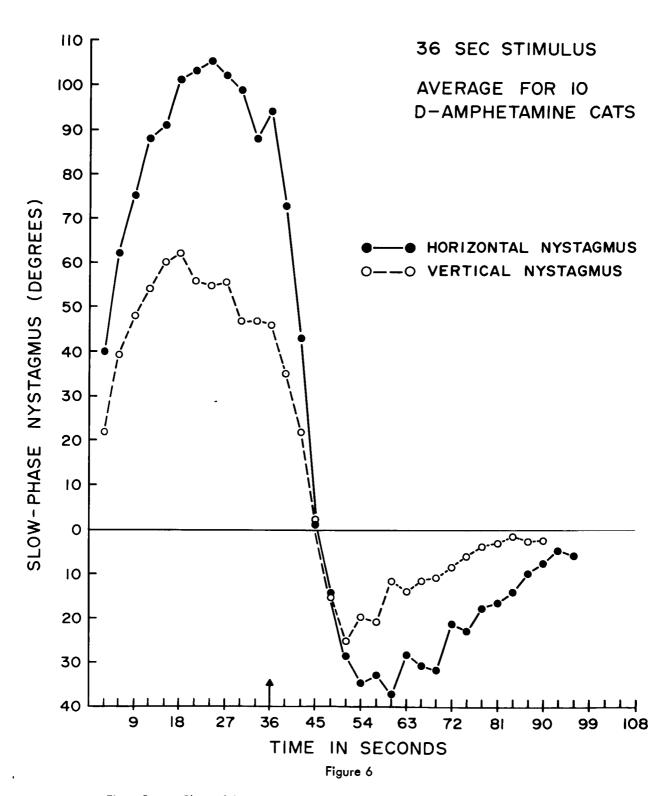
Time-Course Plots of Slow-Phase Eye Displacement in 3-sec Intervals for 8 Human Subjects

differed from cat data: 1) Humans did not show a rise and decline during prolonged (36-second) stimulation whereas the cats did; 2) little or no secondary nystagmic reactions to the 8.4-second stimuli were demonstrated by humans whereas cats consistently gave such responses.

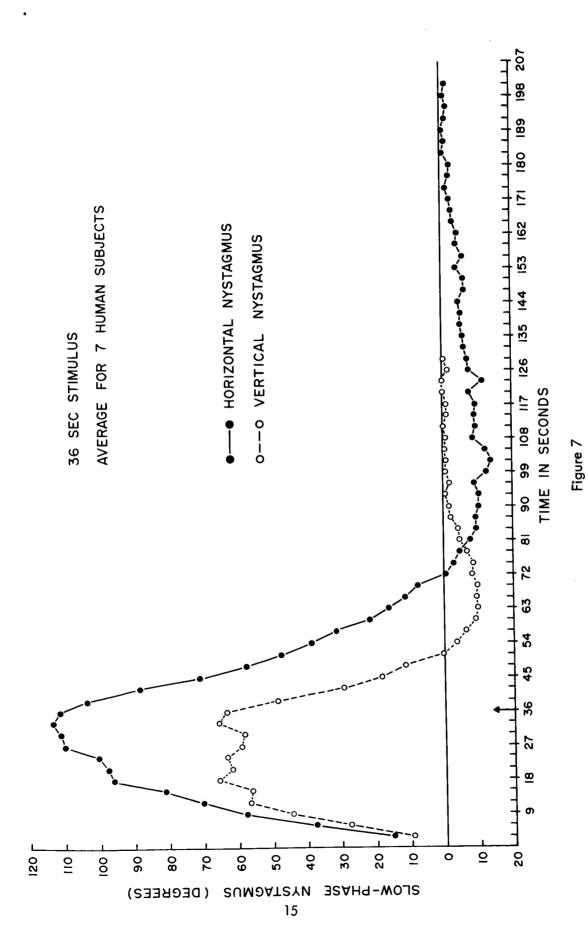
### **AROUSAL**

The importance of grousal on nystagmic responses was noted earlier and has been examined in considerable detail elsewhere (3). To assure reliability of the present data with regard to this factor a second group of ten cats were treated with d-amphetamine in accordance with procedures described by Crampton and Brown (8). Each animal received four trials with each trial comprising an acceleration stimulus of 4 deg/sec<sup>2</sup> for 36 seconds, two minutes of constant velocity, and a subthreshold deceleration (0.15 dea/sec<sup>2</sup>). The first two trials were always stimulation of the lateral canals: the remaining two trials involved vertical canal stimulation. Trials were alternately clockwise (CW) and counterclockwise (CCW). Half the animals began with CW rotation; the remaining five began with CCW rotation. Data from CW and CCW accelerations were similar for the horizontal and the vertical nystaamus curves and, therefore, were averaged. The mean response curves for the ten animals appear in Figure 6 and demonstrate the same type of decline during stimulation and almost identical transition points from primary to secondary nystagmus as those presented by the undrugged cats. Vertical nystagmus again showed a more pronounced decline during stimulation than did horizontal nystagmus. Some supportive neural data for this decline of response during stimulation of the cat have been presented by Cappel (2) who showed plots of single neural unit activity during a prolonged angular acceleration and reported a rise and decline of firing during the stimulus period.

A reliability check of the findings for humans was accomplished by exposing four males and four females, all previously untested, to stimulus conditions (4 dea/sec<sup>2</sup> for 36 seconds) identical to those administered to the other human subjects. Half of the males and females received CW stimulation, the remaining half received CCW rotation. Four trials were administered, two each for the lateral and vertical canals. The first two trials always employed mental arithmetic as an arousal task (3), while in the last two trials the keypress technique of estimating subjective velocity was used to maintain alertness. With the latter technique the subjects attempted to signal successive angular displacements of 90 degrees. Table V contains an outline of the test procedures for this reliability check. Nystagmus data for acceleration and deceleration and for the two tasks showed no evidence of a fall-off in response during stimulation, and the primary-to-secondary nystagmus transition points were almost identical to those obtained under the first set of conditions. The data were thus combined and curves depicting horizontal and vertical nystagmus are plotted in Figure 7. As in the first group of human subjects, no clear evidence for a decline of response during the stimulus is evident. However, the vertical nystagmus time plot does show considerable irregularity as compared with horizontal nystagmus data. Thus, the differences between man and cat that were obtained from the first groups of subjects were confirmed with different subjects and under conditions in which the arousal variable was manipulated.



Time-Course Plots of Primary and Secondary Nystagmus in 3-sec Intervals for Cats
Treated with D-Amphetamine



Time-Course Plots of Primary Nystagmus in 3-sec Intervals for a Second Group of Humans Given Instructions Influencing Arousal During Tests

Table V

Order of Stimulus Presentation for Human Subjects Used in the Reliability Check\*

Sub	ects	Rotation	Mental Arithmetic		Keypress		
Male	Female	Direction	Trial 1	Trial 2	Trial 3	Trial 4	
Α	W	CW	Lateral	Vertical	Vertical	Lateral	
В	X	CCW	Lateral	Vertical	Vertical	Lateral	
С	Υ	CW	Vertical	Lateral	Lateral	Vertical	
D	Z	CCW	Vertical	Lateral	Lateral	Vertical	

<sup>\*</sup>Arousal of subjects was controlled by mental arithmetic and keypress tasks. All trials comprised accelerations and decelerations of 4 deg/sec<sup>2</sup> for 36 seconds separated by 2 minutes of constant velocity.

It has been reported that vestibular nystagmus rises and declines, like the subjective reaction, during constant angular acceleration (1, 17, 20, 22). However, Guedry and Lauver (15) demonstrated that the nystagmic reaction in man did not decline during prolonged constant angular acceleration if the subjects were required to signal estimates of angular displacement. Occasionally, however, a subject would yield a rise and decline in the nystagmus response similar to the subjective responses in earlier experiments (see Figure 4 in Ref. 15). To check the possibility that arousal accounted for the variety of findings, Collins and Guedry (5) required subjects during prolonged angular accelerations to perform mental tasks which would maintain mental activity independently of the subjective perception of rotation. Subjects were required to make arithmetic computations throughout the vestibular stimulation and poststimulation periods. Results showed again that nystagmus first increased and then remained constant during constant angular acceleration. After the termination of stimulation nystagmus decayed about as expected from the torsion pendulum theory (11,21), although rates of decay were not calculated. The same subjects, when allowed to relax, occasionally showed a rise and decline of nystagmus during constant stimulation and a rapid decay of response on termination of the stimulus. The present experiments confirm the fact that nystagmus does not decline during prolonged angular acceleration in alert human subjects, although such declines appear to occur in cats.

In cats, time to <u>onset</u> of secondary nystagmus was inversely related to duration of the stimulus. The <u>earlier onset</u> of the secondary reaction cannot be attributed to loss of arousal. This result strongly suggests that the decline in primary nystagmus

during and after the longer stimuli resulted from a counteracting process which reduced the intensity and duration of the primary nystagmus and then became evident as an early secondary nystagmus. Data from humans have shown that as the duration of a constant angular acceleration is increased beyond certain time limits, the duration of the subjective after-responses becomes shorter and shorter (12, 14). Nystagmic reactions in cats showed similar effects and, in these respects, more closely resembled the subjective reactions of man than they did the nystagmus of man.

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